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COMMUNITY PERTURBATION ASSOCIATED WITH NEW ZEALAND
MUDSNAIL (*POTAMAPYRGUS ANTIPODARUM*) INVASION: DISCREPANCIES IN
TEMPORAL AND SPATIAL ASSESSMENT

By

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B.S., Evergreen State College, Olympia, WA, 2010

Thesis

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COMMUNITY PERTURBATION ASSOCIATED WITH NEW ZEALAND
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TEMPORAL AND SPATIAL ASSESMENT

Chairperson: Dr. Lisa Eby

Invasive species have the potential to alter the ecosystems within which they establish as well as adjacent but uninvaded ecosystems by altering the flow of nutrients or biota across system boundaries. New Zealand mudsnails (*Potamopyrgus antipodarum*; NZMS) are often very abundant where they invade, sequestering the majority of stream primary production. This sequestering of production may reduce aquatic insect production, subsequent insect emergence and subsidies to riparian ecosystems. Tetragnathid spiders, an insectivorous riparian specialist, are dependent on the emergence of aquatic insects and are typical indicators of aquatic insect subsidies to riparian zones. In addition, NZMS invasions can result in persistent community shifts in aquatic insect composition, potentially resulting in lasting impacts to subsidies. We hypothesized that in river sections where they are currently very abundant NZMS would have negative impacts on benthic aquatic insect biomass, reducing the emergence of aquatic insects and spiders that feed on them. We sampled benthic and emerging aquatic invertebrates and tetragnathid spider densities at five locations with various densities of NZMS on two invaded rivers in the Western United States. In the Portneuf River, ID NZMS are currently very abundant while in the Madison River, MT they were abundant fifteen years ago but have since declined. We also analyzed 17 years of benthic community data taken from one location on the Madison River during the NZMS invasion to examine how benthic community composition (and emergent taxa) shifted during peak NZMS densities. In contrast with our expectations, NZMS were positively associated with non-NZMS benthic invertebrate biomass and emergent biomass. Similar to our expectations, spiders had a positive association with emergent biomass and riparian habitat availability. But because of a 200-fold difference in secondary production among sites (sites with high NZMS biomass also had high non-NZMS invertebrate biomass) comparing sites with different densities potentially confounded NZMS density with potential productivity of the site. Examination of time series data of aquatic invertebrate community highlighted that NZMS were associated with lasting changes in benthic community composition marked by reductions in emerging taxa, including Ephemeroptera and Odonata and increases in Baetidae and Tubificidae. Pre-invasion data rarely exist therefore multiple, complementary means of investigation are often necessary to fully evaluate potential impacts of invaders.

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1 **Introduction**

2 Worldwide we are facing an immediate crisis in the maintenance of native biodiversity
3 (Andelman and Willig 2003) caused by a historically unprecedented human-facilitated
4 exchange of biota between landmasses (Vermeij 1996, Vitousek et al. 1996). The spread
5 of invasive species represents one of the most harmful and least reversible of
6 anthropogenic disturbances. Once established, invasive species may alter physical
7 properties of habitats (Loo et al. 2007) and alter native community composition (Moore
8 et al. 2012). Invasive species have also altered biogeochemical cycles, facilitated the
9 invasion of other non-native species (e.g. Vitousek and Walker 1989), caused ‘invasion
10 meltdowns’ through strong community level impacts (e.g. O’Dowd et al. 2003) and
11 modified energy flows through ecosystems (e.g. Baxter et al. 2004).

12 Invasive species have the potential to create perturbations in adjacent but
13 uninvaded ecosystems by altering the flow of nutrients or biota across system boundaries.
14 Specifically, invasive species may have increased competitive ability over native taxa,
15 causing reductions in native consumer densities, and subsequently reducing spatial
16 subsidies to or from neighboring systems (e.g Baxter et al. 2004; Maron et al. 2006;
17 Panchin et al. 2010; Benjamin et al. 2011). Reducing these cross-system energy flows can
18 create substantial changes in community structure because subsidies can bolster
19 populations of consumers at multiple trophic levels in the recipient habitat and are often
20 drivers of biodiversity (Polis et al. 1997). Cross-boundary subsidies between aquatic and
21 riparian systems play an important role in both aquatic and riparian food webs (e.g.
22 Nakano & Murakami 2001), but the effects of invasive species on these flows are rarely
23 considered.

In the few places that it has been examined, studies have found an influence of invasive species on spatial subsidies from the aquatic to the riparian zone. For example, Baxter et al. (2004) and Benjamin et al. (2011) documented the cross-ecosystem effects of stream invasion by rainbow trout (*Oncorhynchus mykiss*) and brook trout (*Salvelinus fontinalis*), respectively. In both systems the invasive trout reduced the production of emergent aquatic insects when compared to stream reaches without invaders and reduced tetragnathid spider density by up to 65 %. Tetragnathid spiders are a useful indicator of aquatic insect emergence because their diet is high in aquatic insects and they track variation in aquatic insect emergence along stream reaches (Gillespie 1987; Power et al. 2004; Marczak & Richardson 2007). Considering effects of invaders on subsidies may be necessary to fully understand the extent of the problems invasive taxa present in these linked ecosystems.

One such invader that may have major impacts on food webs and spatial subsidies is *Potamopyrgus antipodarum* (New Zealand mudsnail, NZMS), a native hydrobiid snail of New Zealand that has invaded aquatic systems throughout the world (Ponder, 1988). NZMS is a generalist grazer of periphyton and vascular plants (Haynes and Taylor, 1984), sharing food resources with many native stream invertebrates. Having a high rate of clonal reproduction (Schreiber et al. 1998), NZMS have been known to reach densities of $\sim 800,000/\text{m}^2$ (Lucas, 1959), but often remain at much lower densities rarely exceeding $1000/\text{m}^2$ in their native range (Holomuzki & Biggs 1999). When they are very abundant, NZMS can sequester the majority of stream primary production (Hall et al. 2003, Hall et al. 2006). Furthermore, where NZMS are at high densities they have been associated with decreased production of native grazing invertebrates (Moore et al. 2012) and dominated

colonization of newly available habitat (Kerans et al. 2005). To date, however, no one has examined whether NZMS reduce spatial subsidies.

Upon invasion some rivers are more prone to having high NZMS density based on their ecosystem characteristics including, calcium availability, temperature, flooding events, and benthic substrate composition. Calcium is necessary for shell development (Herbst et al. 2008) and calcium concentrations are typically high in streams with hot spring contributions. NZMS have reached high densities of over 100,000/ m² on at least three hot spring fed streams in North America: the Madison River (Montana; Kerans et al. 2005), the Portneuf River (Idaho; Hopkins et al. 2007), and Pole Cat Creek (Wyoming; Hall et al. 2003). In addition, NZMS populations are influenced by temperature-dependent development rates (Gust et al. 2011) and high discharge events, as NZMS decreased by over an order of magnitude following irregular flooding in two rivers (Hopkins 2007; Cross et al. 2011). Holomuzki and Biggs (1999) showed that NZMS respond to sheer stress from stream flow by selecting smaller benthic substrate sizes; gravels (diameter 11-28 mm) provided more effective refuge from dislodgment and associated mortality than pebbles (31-60 mm) and cobbles (63-97 mm).

In several documented cases, initial establishment and increase to high NZMS densities have subsequently declined and densities remained low over the longer term, including the Owens River in California (Moore et al. 2012), the Madison River in Montana (Kerans et al. 2005) and the Colorado River in Arizona (Cross et al. 2010; Cross et al. 2011). For example in the Owens River, NZMS declined from 100,000 individuals /m² to fewer than 500 individuals /m² within three years (Moore et al. 2012). During this large fluctuation of NZMS, Moore et al. (2012) discovered shifts in

community composition highlighted by reductions in grazing herbivores and increases in benthic predators and piercing herbivores over the course of a decade. The increase of predator and piercing herbivore biomass persisted after NZMS declined by approximately four orders of magnitude, suggesting that NZMS can induce lasting changes in benthic communities even after their populations have declined and their contribution to community composition was reduced.

Because of the impact exotic NZMS can have on primary and secondary producers, we hypothesized that NZMS will also reduce the flux of aquatic insects to riparian ecosystems where they occur at high densities. We predicted that NZMS biomass would be negatively associated with the biomass of other benthic aquatic invertebrates and emerging aquatic invertebrates. Furthermore, we hypothesized that this reduction in subsidy would have a direct effect on riparian secondary producers and therefore predicted that there would be lower tetragnathid spider densities in areas with higher NZMS biomass. Tetragnathidae build their webs on vertical habitat structure and are positively associated with branch density of understory terrestrial vegetation (Gillepsie 1987). However, the influence of habitat structure on spider density has rarely been investigated as a covariate with prey availability. We predicted that spider density would increase with both habitat availability and aquatic insect emergence.

Because lasting shifts in native benthic communities have been demonstrated (Moore et al. 2012), we also hypothesized that river sections which previously experienced high densities of NZMS (but are now at low densities) are associated with lasting shifts in community composition. We predicted that community changes associated with NZMS will persist in time even after the NZMS population declines by

an order of magnitude or more. If NZMS promote persistent changes in community composition, we predicted that changes might include reductions in the overall representation of emergent taxa in the benthic community given the ubiquitous prevalence of emerging aquatic invertebrate taxa in aquatic ecosystems.

We tested these hypotheses in two North American rivers, the Portneuf River in Southeast Idaho where NZMS occur at high densities and have likely altered community structure (Hopkins 2010) and the Madison River in Southwest Montana where NZMS densities were once abundant and now occur at low densities. Specifically we addressed the following questions to evaluate the impact of NZMS on benthic invertebrate production and cross-system subsidies. Do NZMS alter benthic invertebrate composition and/or reduce benthic invertebrate biomass across river sections in the Portneuf and Madison Rivers across a range of snail densities? Do NZMS reduce aquatic emergence biomass and riparian consumer densities (tetragnathid spiders) across river sections in the Portneuf and Madison Rivers across a range of snail densities? In the Madison River, can we detect persistent impacts in the benthic invertebrate composition after densities decline?

Study areas

We conducted our research on two rivers which both receive geothermally heated spring water, contributing to their potential as good habitat for NZMS. The Portneuf River is a fifth order river and mean annual discharge averaged $6.6 \text{ m}^3/\text{s}$ over the last 100 years, and in 2012 averaged $4.25 \text{ m}^3/\text{s}$ (<http://waterdata.usgs.gov>; gauge 13073000). Sampling areas were at an elevation of approximately 1600 m and the drainage basin of this location is about 1500 km^2 . The Madison River is also a fifth order river formed by the confluence of the

Gibbon and Firehole Rivers within Yellowstone National Park. Mean annual discharge on the Madison averaged $11.8 \text{ m}^3/\text{s}$ over the last 100 years and averaged $14.5 \text{ m}^3/\text{s}$ in 2012 (<http://waterdata.usgs.gov>; gauge 06037500). Sampling locations were at an elevation of approximately 2000 m and at this location the river drains approximately 1100 km^2 .

In the Portneuf River, NZMS were detected in 2000 and by 2004 reached densities of $\sim 1,000,000/\text{m}^2$, likely influencing secondary production. A 6.4-year recurrence interval flood in 2006 disrupted the NZMS population and despite densities diminishing by up to 79 % the rank order of NZMS densities between sampling reaches remained equal between 2004 and 2006 (Hopkins 2007). By 2011 densities had increased to numbers comparable to 2004 (C. Baxter personal communication). Upon comparison with data collected in 1969 and 2004 NZMS were associated with low densities of many native invertebrates, including the aquatic larvae of insects such as Ephemeroptera, Plecoptera and Trichoptera (Hopkins 2007). In addition to NZMS, the native invertebrate community reflected improvements in anthropogenic disturbances including channelization, as well as nutrient and sediment pollution since 1969 (Hopkins, 2010), even though degradation still exists along the river. Furthermore, across locations sampled on the Portneuf River in 2004 Hopkins (2007) found that sites with higher NZMS densities had lower benthic invertebrate densities and taxa richness. Our sampling reaches on the Portneuf River included 5 of 10 of Hopkins (2007) sampling locations with the largest range of NZMS density (2 - 9270 NZMS/colonization basket) and were spread over approximately 50 km in river length (the furthest upstream of Hopkins 2007 sampling locations) (Figure 1 C).

NZMS were first detected in the Madison River in 1995 (Montana PPL unpublished data) and by 1997 reached densities of approximately 300,000/m². In our study site during the last decade, NZMS densities have been documented at over 100,000/m² and dominated colonization of recently available substrate (Kerans et al. 2005, Kerans unpublished data). By 2000 densities began decreasing (PPL unpublished data) and dropped to less than 100/m² by 2007 (Kerans unpublished data). Our sampling reaches on the Madison River were located between the border of Yellowstone National Park and Hebgen Reservoir, where NZMS densities were most variable, totaling a river length of approximately 4 km (Figure 1 B).

Methods

Spatial Comparisons

Within each river study area, we selected five 150 m stream reaches distributed at least 150 m apart to promote independence (Figure 1D). Movements of NZMS are influenced by velocity and resource availability (Sepulveda & Marczak 2011), but documented movements have not exceeded 60 m over 3 months (Adam 1942). Sampling reaches were chosen to include the largest range in NZMS density possible while maintaining as much physical similarity as possible. Within each reach, we sampled benthic biomass and composition, aquatic insect emergence biomass, and spider density.

Benthic Samples:

To determine if non-NZMS benthic invertebrate biomass is associated with NZMS biomass we collected eight benthic samples with a modified surber sampler to

measure biomass of all aquatic benthic taxa. Benthic samples were taken in September 2012 on the Madison River and October 2012 on the Portneuf River. After establishing the upstream and downstream limits of each sampling reach we haphazardly tossed benthic sampling frames into the stream at each 30 m interval. Four benthic samples were collected on each side of the river at depths <1 m and within 3 m of shore to ensure that habitats chosen were at shallow enough depths to received enough sunlight to sustain primary production and minimize habitat variation. Depth at each sampling location was measured and did not fall below 10 cm or exceed 100 cm.

We sampled the benthos from a 0.33 m² area using a modified surber sampler (153 μ m mesh). Because substrate composition is known to influence benthic secondary biomass and diversity (e.g. Minshall, 1984, Quinn and Hickey 1990) we selected visually similar benthic sampling locations by assessing substrate types following the methods of Bisson et al. (1981) and Magee et al. (1996). Additionally, the relative contribution of each substrate type (sand<2 mm, gravel 2-6 mm, pebble 17-64 mm, and bedrock) was recorded as percentage of the total benthic sample for post-collection analysis. The substrate was agitated by hand for 30 seconds and samples were preserved in 70 % ethanol in the field, then picked and sorted in the laboratory. To estimate both non-NZMS benthic invertebrate biomass and NZMS biomass we counted and measured total lengths of individuals for all taxa and converted them to mass using published length-mass relationships (Benke et al. 1999; Hall et al. 2006; Miyasaka et al. 2008; Méthot et al. 2012; Appendix Table 1 for equations used).

181 Aquatic insect emergence

182 To determine if emergent biomass (biomass of aquatic invertebrates with aerial
183 life-stages including the Orders Ephemeroptera, Plecoptera, Trichoptera, Diptera,
184 Odonata, Megaloptera, Hymenoptera, and Coleoptera) is negatively associated with
185 NZMS biomass we placed ten sticky traps to capture and quantify aerial aquatic
186 invertebrates. Each trap was placed 30 m apart (five on each side) in August 2012
187 and September 2012 to account for spatial variability in emergent biomass as
188 suggested by Malison et al. (2010).

189 Emergent biomass was quantified using ten sticky traps at each sampling reach (2
190 8.5" x 10" pieces of acetate, 100 cm² total area) coated with Tanglefoot® (Contech
191 Enterprises Inc. Victoria, BC) mounted on wooden stakes. Stakes were driven into the
192 streambed adjacent to the river's edge where traps were positioned one meter above the
193 surface of the water following Power et al. (2004). During the two sampling periods, we
194 removed the traps after two weeks, covered them with plastic wrap, and froze them.
195 Traps remained frozen until insects were identified to Order except for Diptera, which
196 were identified to family to determine larval origin (aquatic or terrestrial). Total lengths
197 of insects were measured and converted using total length to weight ratios reported in
198 Sabo et al. (2002).

199 Spiders

200 Finally, to determine if riparian spider abundance is negatively associated with
201 NZMS we sampled tetragnathid spider density twice on each river (August and
202 September 2012 on the Madison; July and August 2012 on the Portneuf). We walked five
203 10 m spider transects on each side of the river parallel to stream flow, each transect was

separated by 30 m (Figure 1D). To account for spatial variability in riparian habitat suitable for the building of spider webs we quantified the percentage of each 10 m transect that contained habitat suitable for the building of spider webs (vegetation with vertical structure including tall grasses, woody debris, and shrubs).

We sampled tetragnathid spider abundance at night using high-intensity flashlights starting at about 2200, under complete darkness when spiders are most active (Kato et al. 2003). One observer on each side of the river worked upstream counting all tetragnathid spiders above the active channel and along the riparian zone within two meters of the stream edge and up to a maximum height of 2.5 m.

We visually surveyed availability of spider habitat during spider counts on both rivers. Tetragnathids are orb-weaving spiders and are limited by the availability of riparian vegetation (with vertical structure), which has been shown in both experimental and observational studies (Power et al. 2004, Laeser et al. 2004). Habitat availability was recorded as the proportion of the 10 m sampling area that contained vertical vegetative structure (Figure 4 in appendix for examples). Surveys were taken parallel to the river and within 2 m of the stream bank (10 per reach, five on each side of the river).

Analyses of spatial comparisons

All statistical analyses were performed in R statistical software (R Core Team, 2013). The Madison and Portneuf Rivers were analyzed separately. We compared arcine square-root proportions of three substrate types (sand, gravel, and pebbles) across reaches to determine if there were significant differences in substrate among reaches using single factor ANOVAs. Using the same transformation we then used linear regression and

blocked by reach to determine if substrate composition influenced NZMS and total secondary biomass (biomass \sim proportion sand + gravel + pebbles + cobble).

Then, we tested our prediction that non-NZMS benthic invertebrate biomass and emergent biomass would be negatively associated with NZMS biomass. Non-NZMS benthic biomass, NZMS biomass, and emergent biomass were log-transformed to meet assumptions of normality. For these analyses, we used a linear regression and blocked by reach and month (non-NZMS benthic biomass; emergent biomass; \sim NZMS biomass + month + reach). To examine the possibility that the biomass of some taxa may be affected by NZMS biomass and not others (potentially altering community composition) we conducted similar analyses on the biomass of all Orders of invertebrates found in our benthic samples individually (i.e., Batidae biomass \sim NZMS biomass + month + reach).

To examine whether there was a lower density of tetragnathid spiders adjacent to stream reaches with higher NZMS biomass, we blocked by month and used a quasi-Poisson (link=log) generalized linear model, as suggested by O'Hara (2009) (tetragnathid spider density \sim NZMS biomass + month). To consider the role of both habitat and prey availability on spider density, we again blocked by reach and month and used a quasi-Poisson (link=log) generalized linear model with the formula: (tetragnathid density \sim emergent biomass + proportion of vertical habitat + reach + month) in which the proportion of vertical habitat is that of each 10 m spider transect that contains vegetation that could support spider webs.

Temporal comparison of benthic data

We analyzed annual benthic data collected at one location on the Madison River between 1994 – 2012 to determine if there were shifts in community composition associated with

the NZMS invasion and whether this could influence spatial subsidies. As with other invasive species, NZMS may undergo extensive population fluctuations with an initial build up of high densities which then decline (Kerans unpublished data; Moore et al. 2012). Even as densities decline, non-NZMS benthic biomass may recover, but lasting shifts in community composition have been detected (Moore et al. 2012). We predicted that benthic communities would shift in response to fluctuations in the relative proportion of NZMS and that these changes would include reductions in emerging taxa, potentially altering spatial subsidies.

On the Madison River, we acquired a 17-year data set from Pennsylvania Power and Light (PPL) Montana (August 1994-2012, excluding 2003 and 2004) from a site located within 10 river km of our study area to investigate changes in community composition from first detection to recent years. In this dataset, 3 or 4 0.25 m² modified surber samples were taken. Samples were stored in 70 % ethanol and subsamples of approximately 300 specimens were identified to genus or species by McGuire Consulting, Espanola, NM. These data were reported as composition (proportion of the sample composed of a certain taxon). Changes in NZMS dominated the trends in composition, so we removed them as a confounding factor. Three stages were designated *a priori* as initially low (<10 % NZMS: 1994 and 1995), high (>10 % NZMS; 1996-2001), and decreased (<10 % NZMS: 2002-2012). We aggregated to family level, performed a visual inspection of a Nonmetric Multidimensional Scaling (NMDS; Kruskal and Wish 1978) ordination plot, and ultimately used Multi-response Permutation Procedures (MRPP) to test for significant differences in taxonomic composition between groups (initially low, high, and decreased) (Mielke and Berry 2001).

To determine if community shifts resulted in alteration to spatial subsidies we also aggregated all taxa with emergent adult life stages (Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Odonata) to examine how the proportion of emerging taxa changed in association with the proportion of the community composed of NZMS. We transformed the proportion of native benthic taxa into arcine square-root proportions to meet the assumptions of normality for linear regression. We used a linear regression to explore whether changes in NZMS proportion might result in a reduction in emergent taxa and thus influence aquatic insect emergence. We conducted our analyses using R statistical software (R Core Team, 2013).

Results

Spatial comparisons: Portneuf River

In the Portneuf River differences were found in substrate types among reaches (ANOVA; gravel: $F=3.8$, $p=0.01$; pebbles: $F=2.4$, $p=0.07$; bedrock $F=3.1$, $p=0.02$) but substrate composition had no effect on non-NZMS benthic biomass or NZMS biomass (total; $F=0.39$, $p=0.88$, NZMS; $F=0.82$, $p=0.58$). Sand was similar among reaches (ANOVA; $F=1.8$, $p=0.14$). Average NZMS densities had returned to densities similar to those found by Hopkins (2007) in 2004 and varied between 870-456,000 /m² across study reaches in our benthic samples (reaching >1,000,000 in some samples) and varied between 0.1 to 99 % of benthic secondary biomass. Taxa that emerge (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Odonata, Megaloptera, Hymenoptera, and Coleoptera) never reached more than 9.6 % of total secondary biomass. Average benthic invertebrate biomass varied between 17,000-1,207,400 mg / m² (Figure 2). Variation in total benthic

biomass among samples within reach was very high and differences among reaches were insignificant ($F=0.49$, $p=0.48$). Non-insects (Gastropods, Bivalves, and Crustaceans) dominated total benthic invertebrate biomass (>75 % of total benthic biomass) at all locations.

Our predictions that non-NZMS benthic biomass and emergent biomass would be negatively associated with NZMS biomass were not supported. There was a positive relationship between non-NZMS benthic invertebrate biomass and NZMS biomass ($F=8.16$, $p=0.001$, Figure 2). Furthermore there was no relationship between the biomass of each Order and NZMS biomass when analyzed individually ($p>0.05$ for all taxa). Among reaches, average emergent biomass varied between 41-296 mg/m² and differences between them were significant ($F=3.69$, $p=0.03$), but there was no difference found between months (August and September) ($t=0.3$, $p=0.76$). All emerging taxa that were present in benthic samples were also found as adults on sticky traps (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Odonata, Megaloptera, Hymenoptera, and Coleoptera). There was no relationship between emergent biomass and NZMS biomass ($F= 0.06$, $p = 0.12$, Figure 3). Similarly, our prediction that NZMS biomass would be negatively associated with tetragnathid density was not supported: there was no significant relationship of tetragnathid density with NZMS biomass (GLM: $t=0.54$, $p=0.6$, Figure 4). Surprisingly, tetragnathid density was not predicted either by emergent biomass or habitat availability (GLM: emergence: $t=1.2$, $p=0.98$, habitat: $t=1.7$, $p=0.4$, residual deviance= 7.9).

Spatial comparisons: Madison River

In the Madison River differences were found in substrate types (ANOVA; sand: $F=3.4$, $p=0.02$; pebbles: $F=4.3$, $p=0.007$; gravel $F=3.7$, $p=0.01$) but substrate composition had no effect on non-NZMS benthic biomass or NZMS biomass (total; $F= 1.0$, $p= 0.45$, NZMS; $F= 1.17$, $p= 0.35$,). Average NZMS density varied between 4.5 and 151 individuals/ m² across study reaches in our benthic samples and made up 1 to 3.25 % of benthic biomass. The invertebrate biomass of most benthic samples consisted of over 40 % native gastropods (mostly Physidae). Samples also included five Orders with emergent adult life stages (Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Odonata), and unlike the Portneuf only one sample was composed of less than 30 % emerging taxa. Average total benthic invertebrate biomass did not differ significantly between reaches ($F=2.4$, $p=0.09$).

Our predictions that non-NZMS benthic biomass and emergent biomass would be negatively associated with NZMS biomass were not supported. There was no relationship between non-NZMS benthic invertebrate biomass and NZMS biomass ($F=2.47$, $p=0.068$, Figure 2). Furthermore, there was no relationship between the biomass of each Order and NZMS biomass when analyzed individually ($p>0.05$ for all taxa). Average emergent biomass per reach varied between 3095 and 1150 mg and differences among reaches were significant ($F=3.012$, $p=0.015$); however, there were no differences between months (August and September) ($t=0.897$, $p=0.4$). All five emerging Orders that were found in our benthic samples were also found in our emergence traps (Ephemeroptera, Plecoptera, Trichoptera, Diptera, and Odonata). We expected to see negative associations between emergent biomass and NZMS biomass; however, variance in emergent aquatic insects biomass was not explained by variance in NZMS biomass ($F=1.73$, $p=0.25$, Figure 3).

We predicted that tetragnathid spider density would be negatively associated with NZMS biomass and have a positive relationship with both emergent biomass and habitat availability. In contrast to our predictions, NZMS biomass did not predict tetragnathid density (GLM: $t=-1.2$, $p=0.29$, Figure 4). Emergent biomass did predict tetragnathid density. An increase of 1.5 spiders resulted from a 10-gram increase in emergent biomass per reach, and when considered in conjunction with habitat availability both predictors were significant. Tetragnathids increased by 2.5 individuals per 10 m when vertical spider habitat increased by 10 % (GLM: insect biomass: $t=3.9$, $p=0.007$; vertical habitat: $t=2.786$, $p=0.03$, residual deviance= 2.8).

Temporal comparison of Madison River benthos

NZMS increased from 7 % of taxa present in 1994 to 61.6 % of taxa present in 1996 and then down to <1 % of taxa present by 2012 (Figure 5). Taxonomic composition of invertebrates differed significantly between groups of sampling years that were distinguished *a priori* by stage (initially low, high, and decreased) (MRPP: $A = 0.14$, $p=0.003$; Figure 5). The NMDS ordination stabilized after 8 iterations with a final stress of 10.04.

We aggregated taxa that have emergent adult life stages and found negative associations between % benthic invertebrates that emerge as adults and % NZMS; emerging taxa decreased by 40 % when there was a 70 % increase in NZMS; however, this result was not significant ($t=1.9$, $p=0.06$). We analyzed individual Orders of benthic invertebrates. Of the five Orders that emerge, Ephemeroptera and Odonata had significant negative relationships with % NZMS ($t= -3.04$, $p=0.008$; $t=-3.05$, $p=0.008$,

respectively; Figure 6). Of the other taxa (those which do not emerge) only Annelidae had a significant negative relationship with NZMS ($t = -3.9$, $p = 0.001$).

Discussion

We did not detect any impact of NZMS invaders on trophic linkages between aquatic and riparian communities across our 2012 sampling reaches in either river. NZMS biomass was not negatively associated with non-NZMS benthic biomass or emergent biomass at either river site. In fact NZMS biomass was positively associated with non-NZMS benthic biomass in the Portneuf River and had a similar but statistically insignificant trend in the Madison River. Furthermore no individual Orders of benthic invertebrates had significant relationships with NZMS biomass in our spatial comparisons. This was surprising given the ability of NZMS to consume the majority of primary production where their densities are high (Hall et al. 2003, Hall et al. 2006). In particular, at the Portneuf River study area with average NZMS densities in reaches ranging over 200 orders of magnitude, we expected to detect negative relationships with secondary consumers, which would drive perturbations to riparian consumer communities. Instead we found that NZMS had positive associations with benthic secondary production and no effect on aquatic insects emerging into the riparian zone. In both systems, we were surprised that non-NZMS benthic biomass was highest where NZMS biomass was highest.

We considered two potential reasons that NZMS were not negatively associated with benthic or emergent invertebrates on either river. First, we considered the possibility that NZMS may be occupying novel or previously unoccupied niches within the benthic community. Although there is little consensus on the existence of vacant niches (see

Herbold & Moyle 1986), there are numerous examples of invaders having no measurable effect on native communities (i.e. Simberloff 1981). Some researchers have claimed that invasive species can take advantage of unoccupied niches and have no effect on sympatric species (i.e. Cizek et al. 2003), but the high diet and spatial overlap that NZMS have with multiple grazing benthic herbivores in our systems make this unlikely.

We also considered the possibility that differences in the capacity for secondary productivity between locations may be overpowering any effects NZMS have on benthic and emergent invertebrates. Given that non-NZMS benthic biomass differed 200-fold among sites, it is probable that variation in benthic consumer biomass (including NZMS) is in response to variation in one or more environmental variables. Furthermore we found a positive association between NZMS biomass and non-NZMS benthic invertebrates both across sampling reaches and within many of the reaches individually (see appendix figures 8 and 9). This suggests that such large differences in NZMS biomass are in response to differences in the capacity for secondary production. NZMS comprised 99 % of secondary benthic biomass at many locations on the Portneuf; what is unknown is what proportion of the biomass usurped by NZMS would be assimilated by other benthic consumers in the absence of NZMS, more specifically by those that would emerge as adults. If this proportion were substantial, NZMS would be having large impacts on aquatic emergence. Because of such large differences in secondary biomass we find it probable that NZMS are negatively affecting non-NZMS benthic invertebrate biomass at each sampling location, but have a positive relationship with non-NZMS invertebrates across our sampling reaches.

Emergent biomass and habitat availability had no association with Portneuf River tetragnathid spiders but did have significant effects on tetragnathid density on the Madison. The Portneuf is in general more disturbed (surrounded by agriculture and human development) than the Madison (which flows out of Yellowstone National Park) and we speculate that spiders may be more influenced by agricultural activity and increased habitat removal than by prey availability on the Portneuf. It is possible that we need to account for multiple stressors on the Portneuf (i.e., total impacts) or account for a wider range of habitat differences.

On the Madison River, we found that tetragnathids have a positive association with aquatic prey availability and the percentage of habitat suitable for web building. Only two of the studies we found examining the association between tetragnathid density and their prey included a measure of riparian habitat structure (Chan et al. 2009; Benjamin et al. 2011), but it was not a significant predictor of tetragnathid density in either case. The other studies we reviewed which examined tetragnathid spiders did not account for web-building habitat in their models (Gillepsie 1987; Kato et al. 2003; Baxter et al. 2004; Iwata 2006; Marczak & Richardson 2007; Paetzold et al. 2014). However, tetragnathids have responded positively to experimentally increased habitat availability (Chan et al. 2009). In addition, Iwata (2007) found that densities of spiders from the family Linyphiidae were significantly higher in riparian areas near pools than riffles, and this was only true when accounting for shrub density in his model. Our findings, and those of Iwata (2007), indicate that quantifying both prey at a smaller scale (in stream habitat unit) as well as spider habitat availability may improve models that investigate this kind of relationship and should be considered in future studies. We speculate that the relationship

between tetragnathids and habitat suitable to build their webs is ubiquitous in riparian areas where they are present because of their need to build webs to obtain emerging aquatic insects. Furthermore this indicates that multiple stressors may compound the impacts of invasive species on native communities. For instance, if riparian spiders *are* in fact reduced by alterations in prey availability due to invasive aquatic species this effect may be intensified or hidden to the observer by the presence of other disturbances such as habitat removal.

Although we did not find an effect of NZMS biomass on non-NZMS benthic biomass among sites, we did find that NZMS altered benthic community composition at one location over the course of 18 years. Our multivariate analysis indicated not only a shift in benthic species composition associated with high proportions of NZMS, but potential lingering changes in community composition that persisted in time as our reduced NZMS community did not resemble the initially-low NZMS community. Each stage of invasion had a distinct community assemblage as indicated by separation in ordination space. Additionally as NZMS proportions declined, some emergent taxa (i.e., Ephemeroptera and Odonata) comprised a higher proportion of benthic samples as seen in our linear regressions for this data. This is not conclusive evidence that NZMS reduce the overall biomass of these Orders. Certainly, other Orders could have increased along with NZMS during this time period, leaving Ephemeroptera and Odonata as smaller proportions of the community. However, given what we know about the feeding habits of NZMS (Hall et al. 2003, Hall et al. 2006), and their impact on benthic taxa in other systems (i.e. Kerans et al. 2005, Moore et al. 2012), we find it likely that NZMS were negatively related to the *abundance* of these Orders. Interestingly we found no similar negative relationship with

any Order of benthic invertebrate and NZMS biomass in our spatial data from the Madison or Portneuf Rivers. Again we find it likely that any affect NZMS may have on the biomass of benthic invertebrates in these systems, even when investigating individual taxa, may be overpowered by the large differences in the capacity for secondary production among sampling locations. Because of the discrepancies we found between our spatial and temporal analyses we suggest caution when using spatial comparisons for investigating the impacts of invaders when temporal data is unavailable.

In addition to potentially reducing the abundance of emergent taxa, long-term shifts in community composition in the Madison River may indicate a phase-shift to an alternative stable state. Alternative stable states may occur when environmental perturbations modify community composition from one stable state to another (Beisner et al. 2003). Years that we designated as ‘reduced years’ grouped tightly in our ordination (Figure 5) and were associated with increased percentages of Baetidae and Tubificidae. Reduced NZMS years may be representing a new stable-state which are significantly different from high NZMS density years and initially low years (MRPP: $A=0.14$, $p=0.003$). If the changes in community composition that we have reported in the Madison are driven by NZMS it may indicate that NZMS can create phase shifts in vulnerable rivers marked by increases in Baetidae and Tubificidae, which could potentially have subsequent impacts. For instance, some species of Tubificidae worms can serve as a secondary host for *Myxobolus cerebralis*, the myxozoan parasite responsible for causing whirling disease in salmonid fish (Gilbert and Granath 2003) and increases in tubificids could potentially lead to increased risk of whirling disease.

Assessing the impacts of invaders is challenging for several reasons including:
pre-invasion data on biota of interest is often limited or non-existent, perturbations can be
indirect (i.e. spatial subsidy alterations), perturbations may occur over many years and
can only be identified with repeated sampling, and the impacts of invaders may be cryptic
or altered due to multiple disturbances (i.e. invaders + habitat loss). It is common that
pre-invasion data and reference sites do not exist for many invaded systems and because
of this we suggest a need for complementary approaches such as *in situ* experiments,
spatial comparisons, and analyzing long-term datasets. Even though they may be difficult
to locate, datasets from state and federal agencies, and non-governmental organizations
may be available and can prove to be very valuable in assessing environmental impacts.

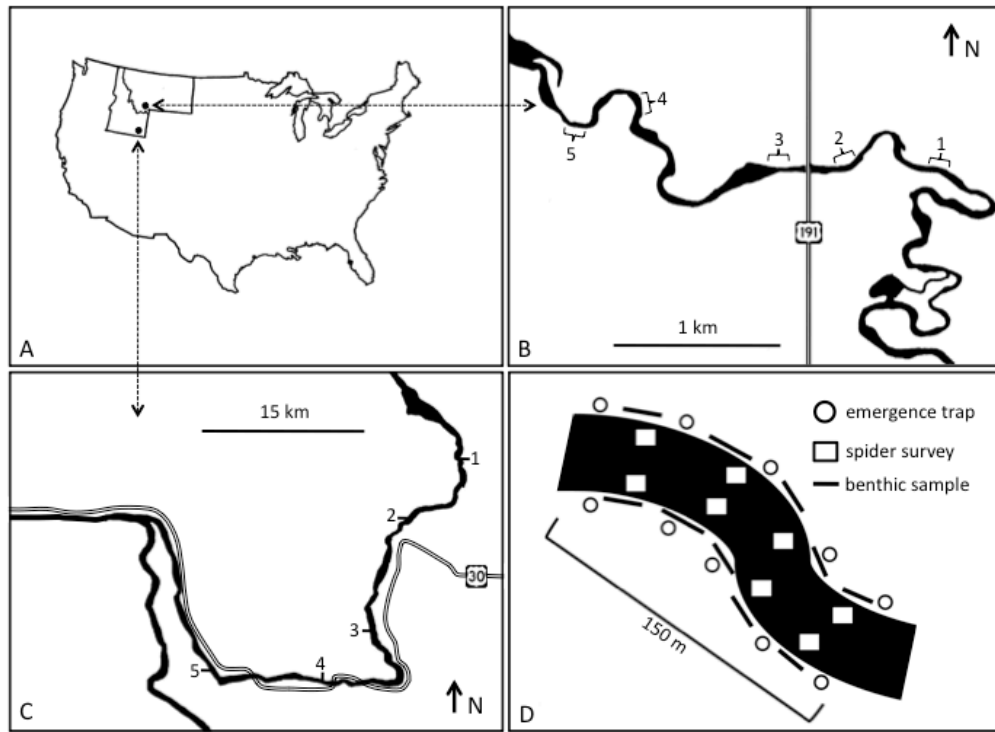


Figure 1: Dots representing the locations of the Portneuf River, Idaho and the Madison River, Montana. B.) Map of sampling reaches on the Madison River, Montana. C.) Map of sampling reaches on the Portneuf River, Idaho. D.) Diagram of sampling design on each reach (one of 5 on each river).

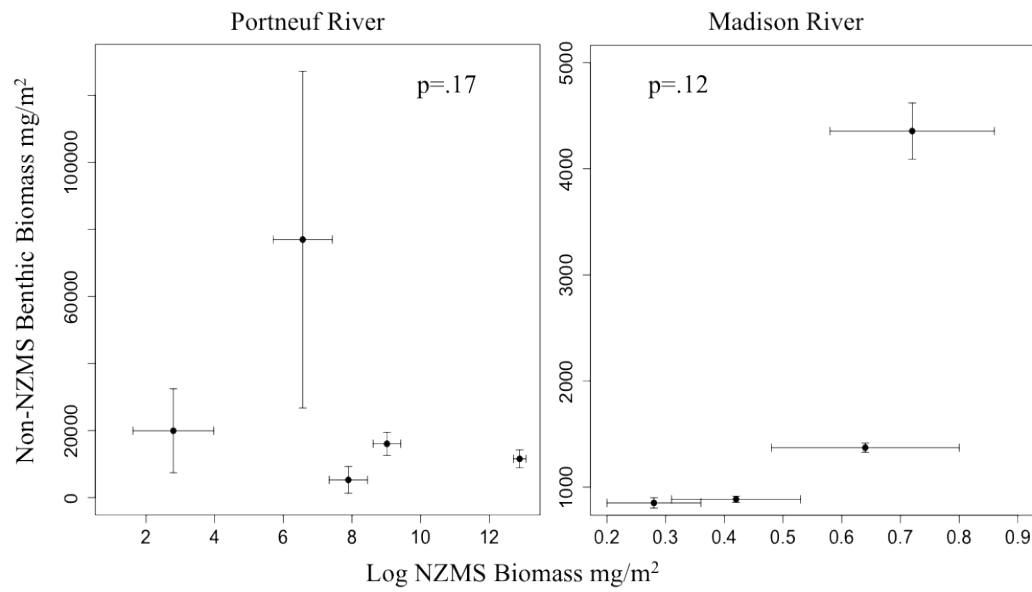


Figure 2: Non-NZMS benthic biomass at various biomasses of NZMS. No relationship was found between NZMS biomass and non-NZMS benthic biomass on either the Madison or the Portneuf River ($F=1.62$, $p=0.17$; $F=2.04$, $p=0.12$ respectively).

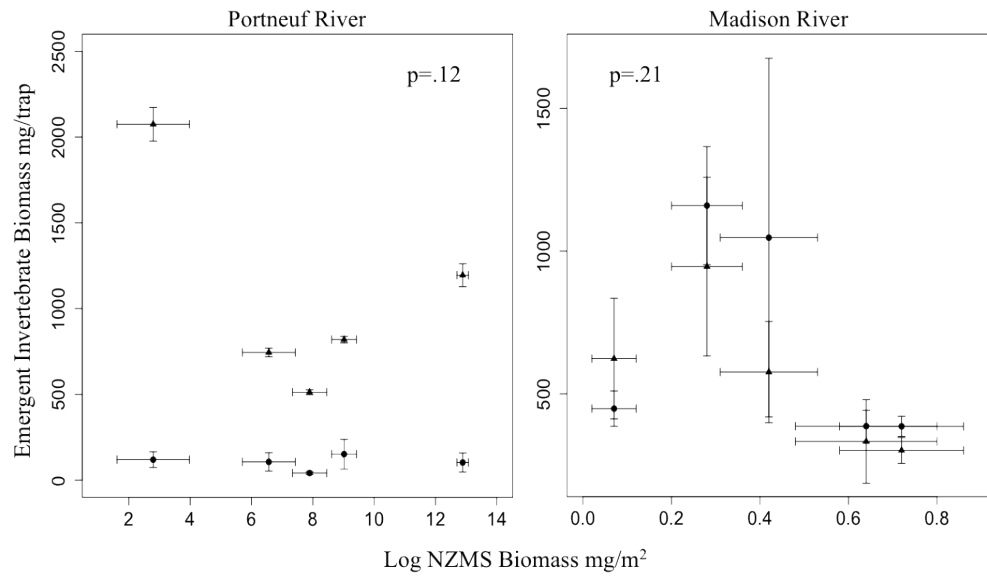


Figure 3: Emergent aquatic invertebrate biomass (Ephemeroptera, Plecoptera, Trichoptera, Diptera, Odonata, Megaloptera, Hymenoptera, and Coleoptera) at various densities of NZMS. No relationship was found between NZMS biomass and emergent biomass on either the Portneuf or the Madison River ($F=0.06$, $p=0.1$; $F=1.7$, $p=0.21$ respectively).

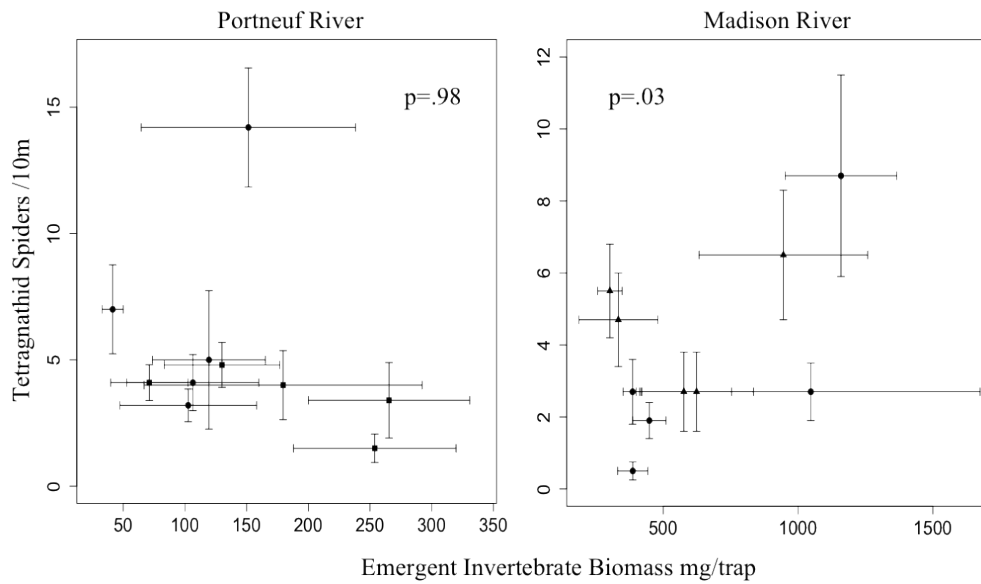
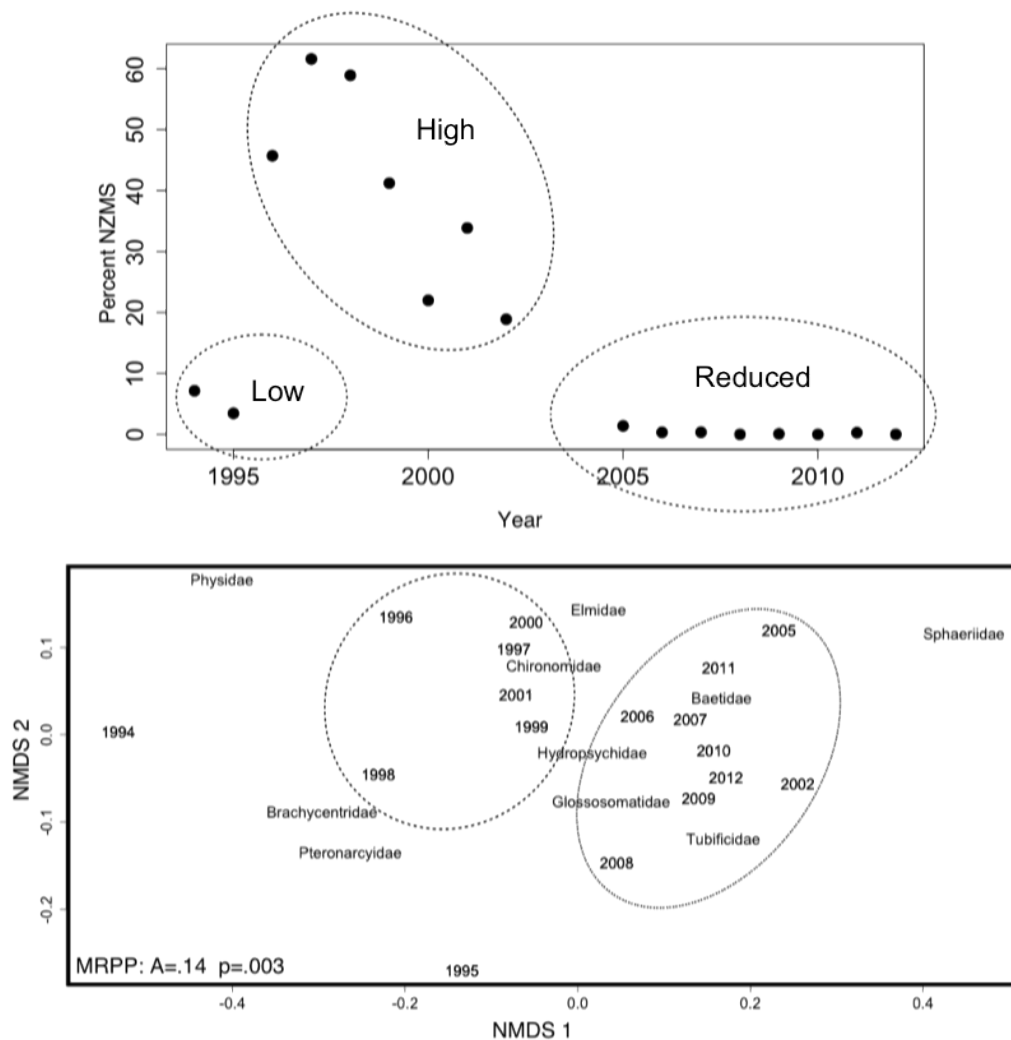


Figure 4: Tetragnathid spider density as a function of emerging aquatic insect biomass. Variation in tetragnathid density was explained by variation in emergence on the Madison River ($t = 2.9$, $p=0.03$) but not the Portneuf River ($t=1.2$, $p=0.98$).



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510 Figure 5: 17 years of benthic invertebrate compositional sampling began in 1994 when
 511 NZMS were first detected and were collected during large fluctuations of NZMS.
 512 Samples were categorized *a priori* by stage of invasion as: initially low, high, and
 513 decreased. Overall percentage of individuals in samples that were NZMS per year is
 514 presented in the top panel. A non-metric multi-dimensional scaling ordination (bottom
 515 panel) was conducted on these data organized at the Family level. Years represent each
 516 round of sampling and also a unique benthic community in the ordination. Samples
 517 clustered in accordance with the stage we determined *a priori* and the differences
 518 between their placement in ordination space were significant (MRPP $A=.14$, $p=.003$).

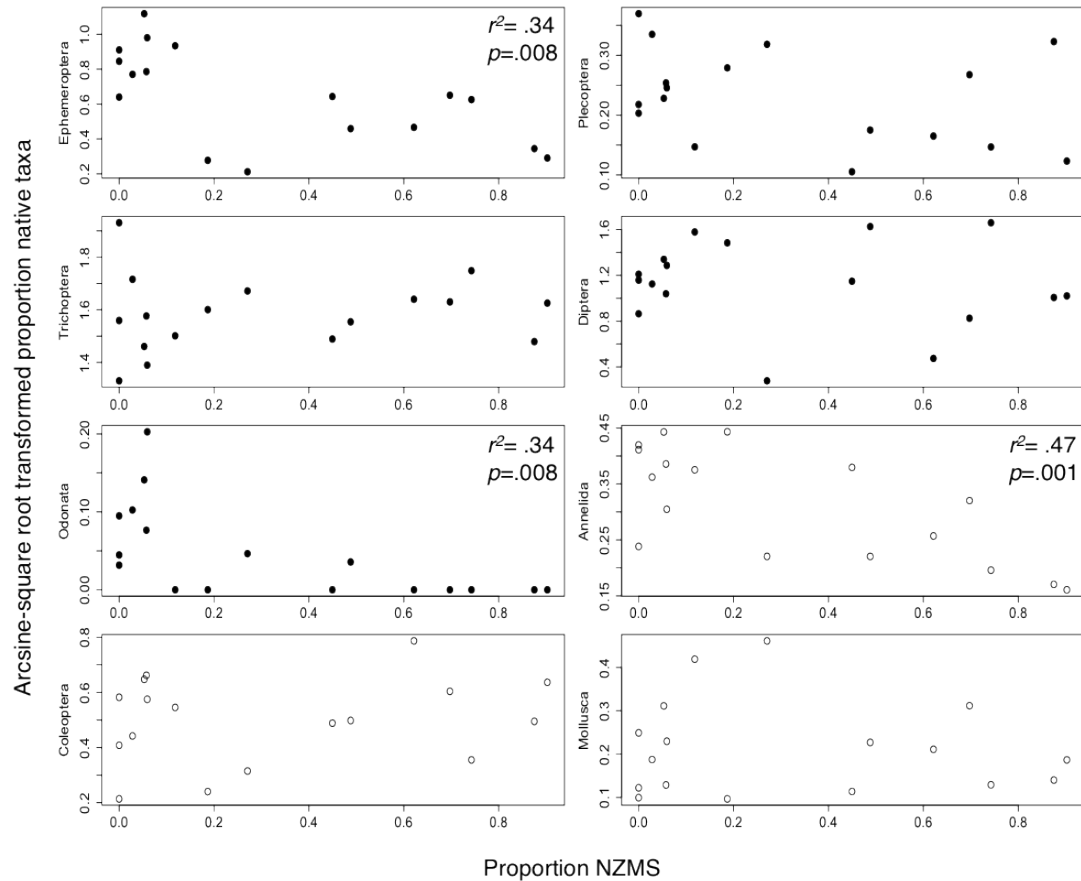


Figure 6: Arcsine-square root transformed proportion of benthic invertebrates excluding NZMS (organized by at the family level) as a function of the proportion of NZMS per sampling year. Data were collected each August from the same location on the Madison River for 18 years during large fluctuations of NZMS density. Taxa with emergent life stages are represented with closed circles and those that do not emerge are represented with open circles. Linear regressions were conducted and significant relationships are presented with r^2 and p values.

Appendix

Table A1: Regression equations used to estimate benthic invertebrate dry mass and ash-free dry mass from total lengths of benthic taxa. Coefficients a and b are used in equations where DM= Dry mass, AFDM= ash-free dry mass, and L= total length.

Taxa	Coefficient a	Coefficient b	Equation	Authors
Ephemeroptera	0.0071	2.83	DM= aL^b	Benke et al. 1999
Plecoptera	0.0094	2.75	DM= aL^b	Benke et al. 1999
Tricoptera	0.0056	2.839	DM= aL^b	Benke et al. 1999
Diptera	0.0025	2.692	DM= aL^b	Benke et al. 1999
Odonata	0.0078	2.792	DM= aL^b	Benke et al. 1999
Coleoptera	0.0077	2.91	DM= aL^b	Benke et al. 1999
Crustacea	0.087	3.015	DM= aL^b	Benke et al. 1999
Physidae	-1.34	3.05	$\log_{10}DM = \log_{10}a + b(\log_{10}L)$	Méthot et al. 2012
NZMS	0.0199	2.375	AFDM= aL^b	Hall et al. 2006
Bivalvia	0.0163	2.477	DM= aL^b	Benke et al. 1999
Annelidae	0.008	1.88	DM= aL^b	Miyasaka et al. 2008
Hemitera	0.0108	2.734	DM= aL^b	Benke et al. 1999
Megaloptera	0.0037	2.838	DM= aL^b	Benke et al. 1999

Table A2: Published regression coefficients used to estimate dry mass of emergent aquatic insects from Sabo et al. 2002 in equation $DM=aL^b$ where DM= dry mass and L= total length.

Taxa	Coefficient a	Coefficient b
Ephemeroptera	0.014	2.49
Plecoptera	0.26	1.69
Odonata	0.14	2.27
Coleoptera	0.04	2.64
Megaloptera	0.1	2.37
Trichoptera	0.01	2.9
Hymenoptera	0.56	1.56
Diptera -Chironomidae	0.04	2.26
Diptera -Simuliidae	0.04	2.26
Diptera -Tipullidae	0.04	2.26
Diptera -Culicidae	0.04	2.26

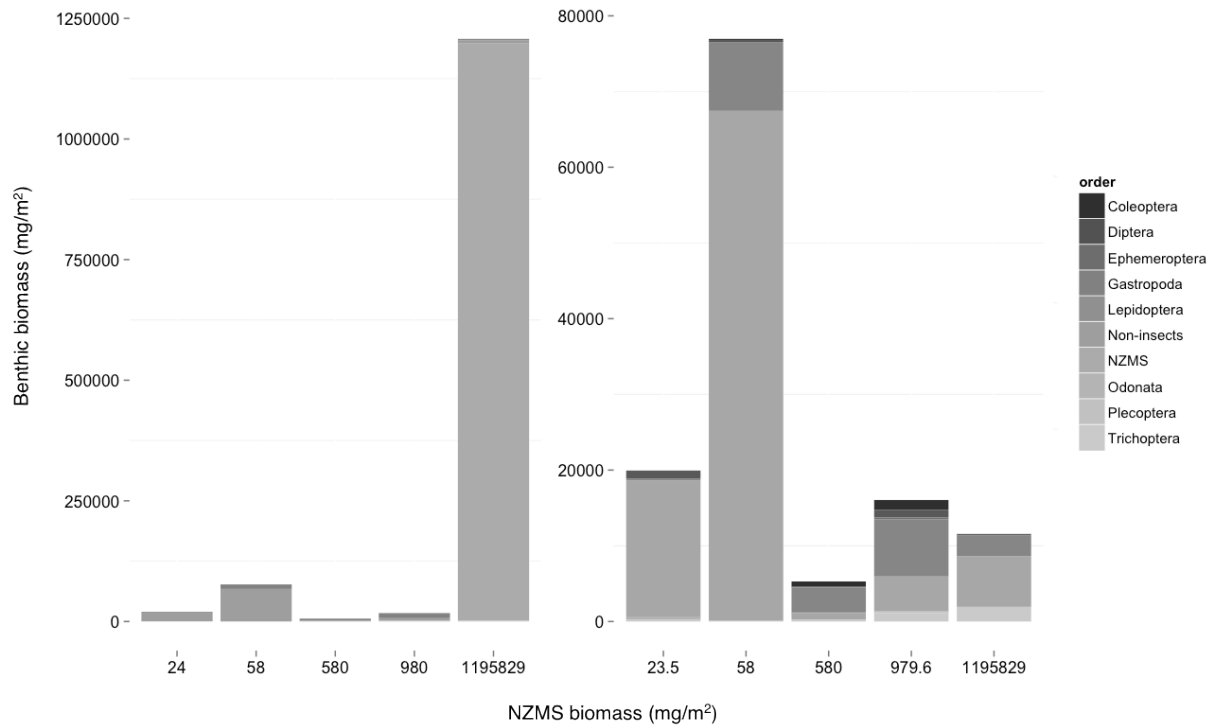


Figure A 1: Portneuf River benthic invertebrate biomass and relative abundance of taxa present in samples at each sampling reach organized by NZMS biomass on the x-axis. The panel on the left includes NZMS biomass in the y-axis and the right hand panel does not.

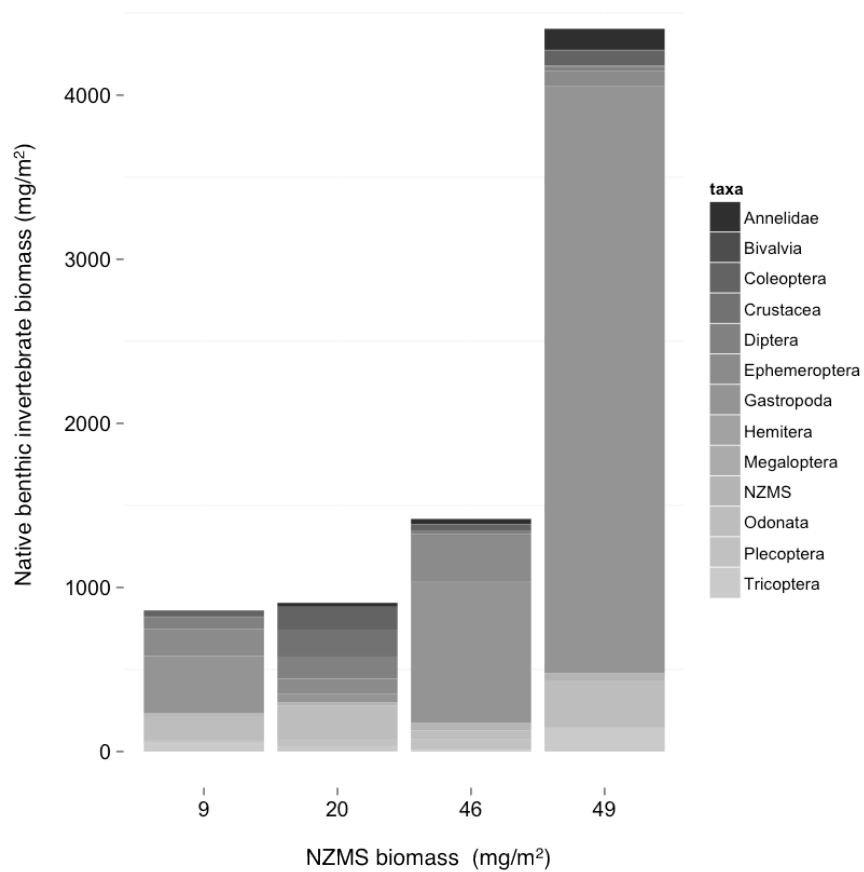


Figure A 2: Madison River benthic invertebrate biomass and relative abundance of taxa present in samples at each sampling reach organized by NZMS biomass on the x-axis.

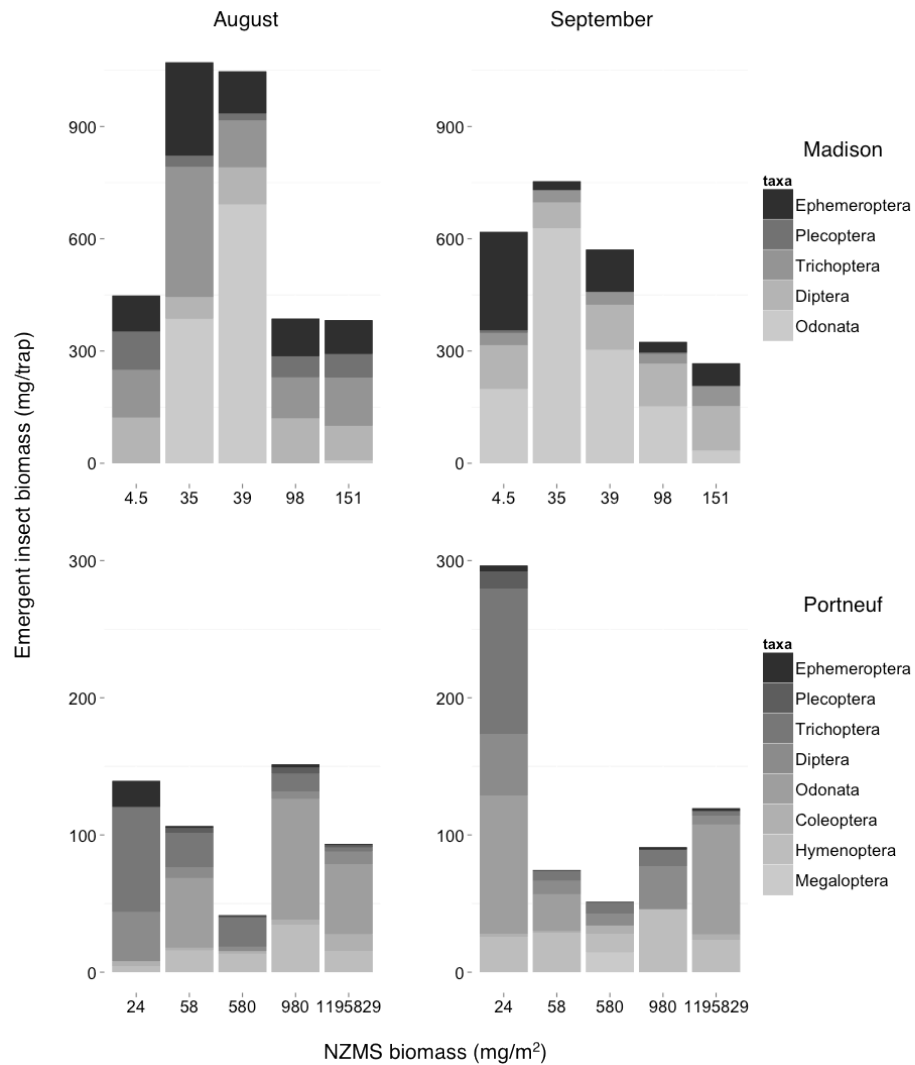


Figure A 3: Emergent insect biomass and relative abundance of each taxa taken from sampling reaches on the Portneuf and Madison Rivers in August and September 2012. Data are organized on the x-axis by NZMS biomass from adjacent benthic samples.



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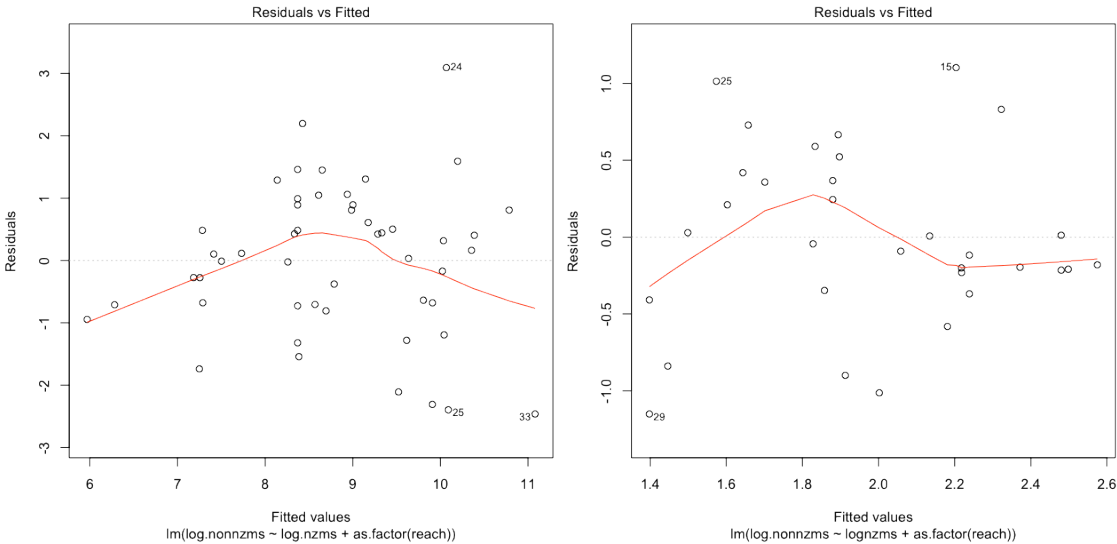
Figure A 4: Examples of low (top) and high (bottom) habitat availability to riparian spiders on the Madison River.

Table A3: Portneuf (top) and Madison River (bottom) linear model formulas and results estimating non-NZMS benthic biomass from log NZMS biomass plus sampling reach as a blocking factor.

Formula =	Log(Portneuf native benthic biomass)~Log(NZMS biomass) + sampling reach as factor			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	8.37	0.42	20.11	< 2e-16
NZMS	0.38	0.09	4.19	0.000132
Reach 2	-1.33	0.68	-1.95	0.058
Reach 3	0.28	0.58	0.48	0.63
Reach 4	-3.5	1.01	-3.44	0.0013
Reach 5	-3.09	0.65	-4.72	2.42e-05
Residual standard error: 1.253 on 44 degrees of freedom				
<i>F</i> -statistic: 8.16 on 5 and 44 degrees of freedom; <i>p</i> = 1.617e-05				
Multiple R^2 : 0.48		Adjusted R^2 : 0.42		

Formula =	Log(Madison native benthic biomass)~Log(NZMS biomass) + sampling reach as factor			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	1.8	0.29	6.16	1.4e-06
Log NZMS	0.46	0.32	1.42	0.16
Reach 3	0.17	0.31	0.55	0.59
Reach 4	-0.14	0.31	-0.42	0.68
Reach 5	-0.43	0.33	-1.34	0.19
Residual standard error: 0.61 on 27 degrees of freedom				
<i>F</i> -statistic: 2.47 on 4 and 27 degrees of freedom; <i>p</i> = 0.068				
Multiple R^2 : 0.27		Adjusted R^2 : 0.16		

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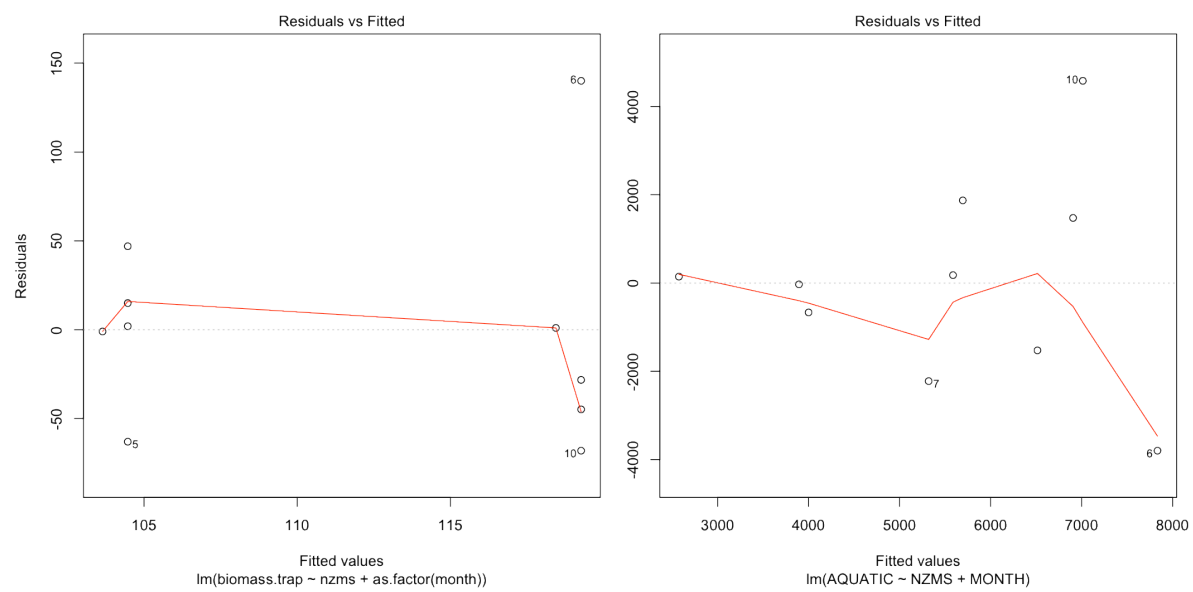
Figure A 5: Residual vs. fitted plots for the Portneuf (left) and Madison Rivers (right) corresponding with the linear models in table 3.

Table A4: Portneuf (top) and Madison River (bottom) linear model formulas and results estimating emergent insect biomass from log NZMS biomass plus sampling month as a blocking factor.

Formula =	Portneuf emergent biomass~NZMS biomass + month as factor			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	104.5	32.8	3.18	0.02
NZMS	-6.888e-07	4.572e-05	0.77	0.99
Month	14.8	43.7	0.59	0.75
Residual standard error: 69.14 on 7 degrees of freedom				
<i>F</i> -statistic: 0.06 on 2 and 7 degrees of freedom; <i>p</i> = 0.12				
Multiple <i>R</i> ² : 0.02		Adjusted <i>R</i> ² : 0-0.27		

Formula =	Madison emergent biomass~NZMS biomass + month as factor			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	7954.6	1576.99	5.04	0.001
NZMS	-26.9	15.95	-1.69	0.14
Month	-1319.3	1670.78	-0.79	0.46
Residual standard error: 2642 on 7 degrees of freedom				
<i>F</i> -statistic: 1.734 on 2 and 7 degrees of freedom; <i>p</i> = 0.25				
Multiple <i>R</i> ² : 0.33		Adjusted <i>R</i> ² : 0.14		

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644 Figure A 6: Residual vs. fitted plots for the Portneuf (left) and Madison Rivers (right)
645 corresponding with the linear models in Table 4.

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646
 647 Table A5 Portneuf (top) and Madison River (bottom) linear model formulas and results
 648 estimating tetragnathid spider density from log emergent insect biomass plus the
 649 proportion of the transect with spider habitat plus sampling month as a blocking factor.

Formula =	Portneuf spiders~emergent biomass+prop habitat+month, Family=quasipoisson(link= log)			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	0.47	0.95	0.94	0.64
Emergent biomass	0.01	0.01	1.2	0.98
Proportion habitat	0.02	0.01	1.72	0.4
Month	-1.12	0.52	-2.15	0.07
Null deviance: 17.2 on 9 degrees of freedom				
Residual deviance: 7.91 on 6 degrees of freedom				

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Formula =	Madison spiders~emergent biomass+prop habitat+month, Family=quasipoisson(link= log)			
	Estimate	Standard error	<i>t</i> -value	<i>p</i>
Intercept	-1.8	.8	-2.3	0.06
Emergent biomass	0.00015	0.0000.4	3.9	0.007
Proportion habitat	2.5	0.9	2.8	.03
Month	0.6	0.23	2.5	0.04
Null deviance: 14.2 on 9 degrees of freedom				
Residual deviance: 2.8 on 6 degrees of freedom				

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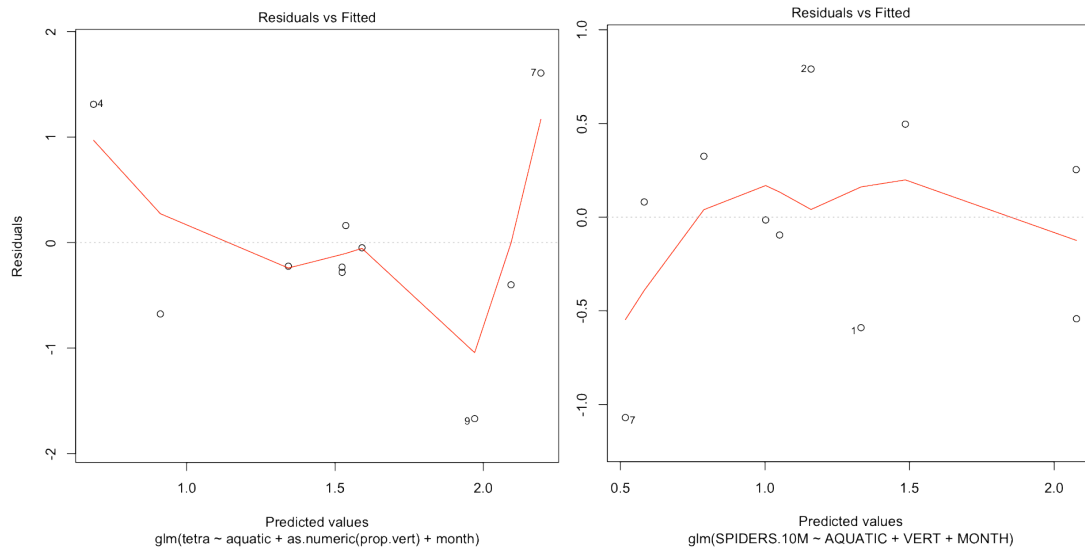


Figure A 7 Residual vs. fitted plots for the Portneuf (left) and Madison Rivers (right) corresponding with the linear models in Table 5.

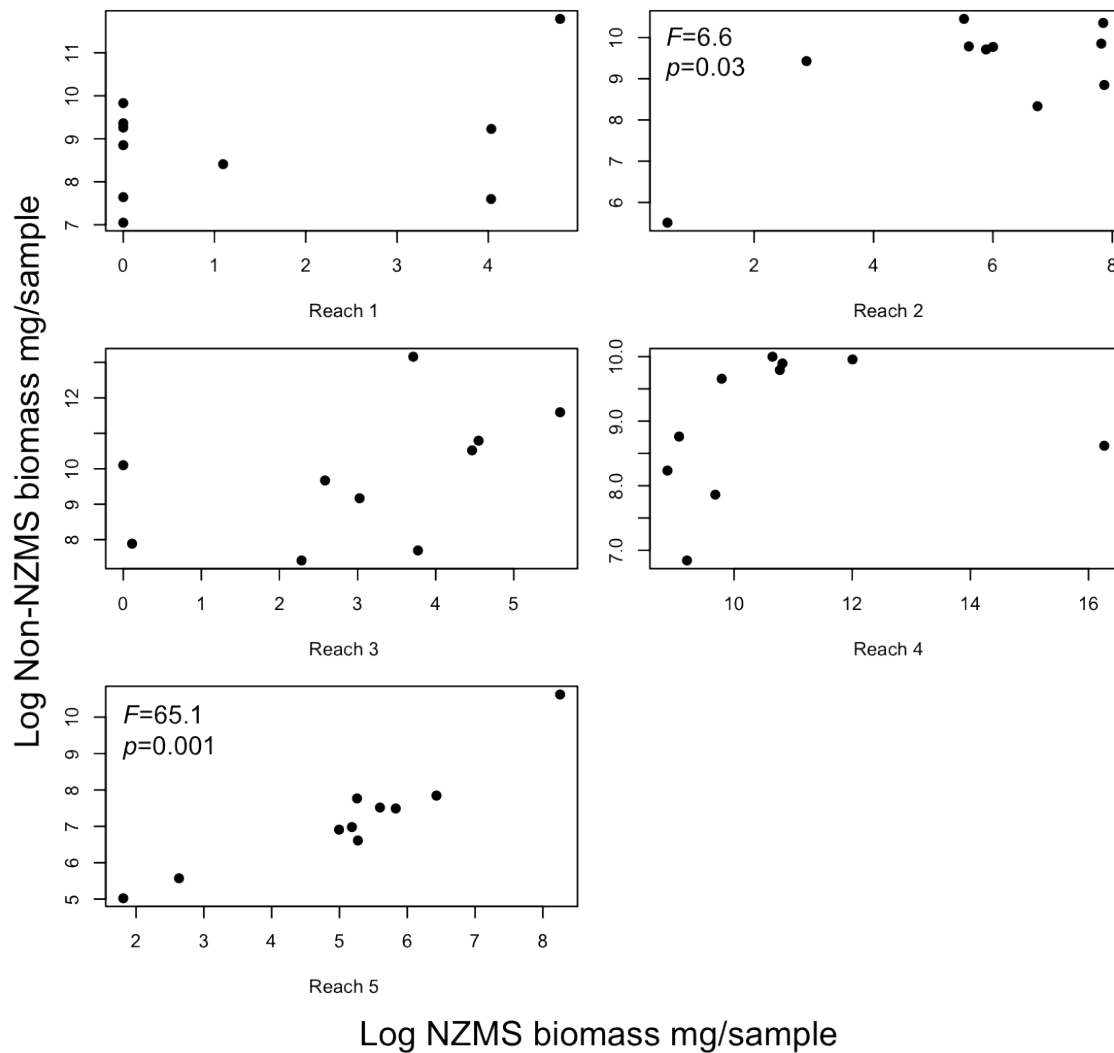


Figure A 8 Portneuf River relationships between log-transformed Non-NZMS and log-transformed NZMS biomass at the sampling reach scale. Each reach was analyzed individually using normal linear regression and significant relationships are reported.

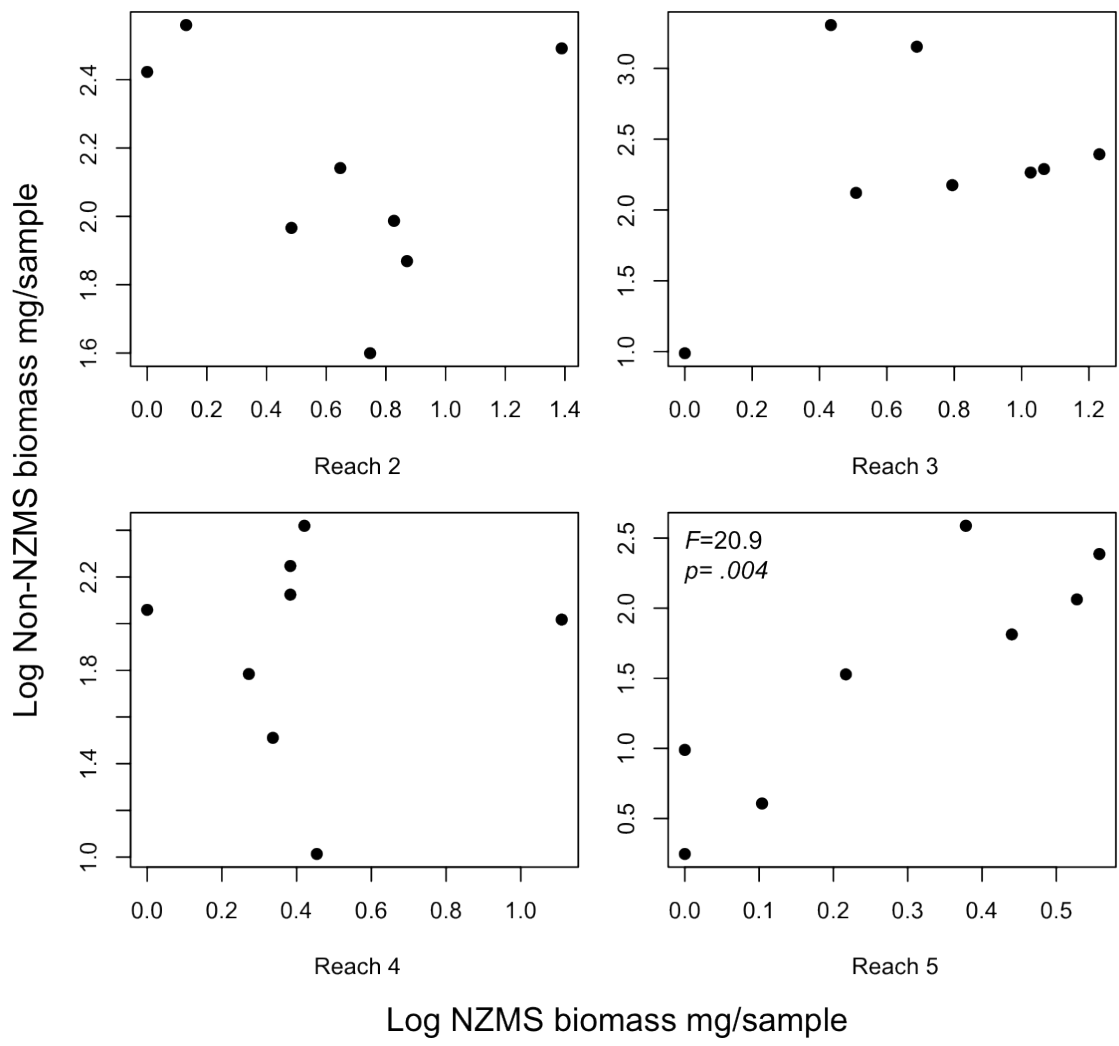


Figure A 9 Madison River relationships between log-transformed Non-NZMS and log-transformed NZMS biomass at the sampling reach scale. Each reach was analyzed individually using normal linear regression and significant relationships are reported.

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